

Megalastrum (Dryopteridaceae – Pteridophyta) in Bolivia, with Descriptions of Six New Species

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ABSTRACT.—A treatment of *Megalastrum* (Dryopteridaceae - Pteridophyta) is provided for Bolivia. We recognize 14 species, of which six are described as new: *M. alticola*, *M. aureisquama*, *M. bolivianum*, *M. ciliatum*, *M. marginatum*, and *M. rupicola*. Also provided are notes and selected specimen citations for the other species, and a key to all Bolivian species of the genus.

Megalastrum (Dryopteridaceae) was described by Holttum (1986) to accommodate species placed by Christensen (1913, 1920) in his informal species group of *Dryopteris subincisa* within *Dryopteris* subg. *Ctenitis*. *Megalastrum* is distinguished from related genera, in particular *Ctenitis*, by venation and indument characters. In *Megalastrum*, the basal basispic veinlets of the distal pinnules arise from the penultimate axes (not from the ultimate axes) and the basispic lobes of the distal pinnules of 2-pinnate-pinnatifid blades are therefore broadly adnate to the costae. Furthermore, in *Megalastrum* the veins end before the margins in conspicuous clavate tips, as viewed adaxially. On the adaxial axes, *Megalastrum* has coarse, whitish, septate, pointed, antrorsely strigose or spreading hairs, whereas *Ctenitis* and other related genera have fine, usually blunt, reddish, erect to spreading hairs in which the dried cells usually collapse. Transfers of 39 neotropical species previously placed in *Dryopteris* or *Ctenitis* into *Megalastrum* were made by Smith & Moran (1987).

Although *Megalastrum* is nowadays accepted as a distinct genus (e.g., by Tryon and Stolze 1991, Smith and Moran 1995), its species-level taxonomy remains poorly known. The last treatment of the neotropical species now placed in *Megalastrum* was by Christensen (1920), and the genus is in urgent need of monographic treatment (Smith and Moran 1987, 1995). The taxonomy of *Megalastrum* is particularly difficult because herbarium material is usually incomplete due to the large size of many species. During taxonomic work for a forthcoming pteridophyte flora for Bolivia, we have studied 110 gatherings of *Megalastrum* from Bolivia and recognize 14 species, of which six are here described as new. We also provide comments on the remaining Bolivian species of the genus, as well as a key to all Bolivian species. In the case of two widespread species, *M. pulverulentum* and *M. subincisum*, extensive morphological variability leads us to believe that species complexes may be involved. As this situation requires the examination of material from the entire ranges of these taxa, which would have exceeded the scope of this study, we refrain from subdividing or recircumscribing them.

KEY TO THE BOLIVIAN SPECIES OF MEGALASTRUM

1. Blades pinnate-pinnatifid; basispic pinnules of proximal pinnae sometimes pinnatifid
 2. Costules and veins abaxially with whitish hairs 0.5–1 mm long **2. M. bolivianum**
 2. Costules and veins abaxially glabrous or with very few hairs 0.1–0.3 mm long
 3. Rachises densely puberulent; rhizome scales orange to medium brown under magnification and strong light, brown en masse **1. M. biseriale**
 3. Rachises glabrous or sparsely puberulent; rhizome scales dark brown
 4. Rachis scales linear, dark brown; sori inframedial **3. M. honestum**
 4. Rachis scales broadly lanceolate, pale brown; sori suprasedial **4. M. yungense**
1. Blades 2-pinnate or more divided
 5. Indusia present
 6. Indusia 0.1–0.3 mm in diameter; blades abaxially with short hairs between the veins **5. M. adenopteris**
 6. Indusia 0.8–1 mm in diameter; blades abaxially glabrous or nearly so between the veins **14. M. villosulum**
 5. Indusia absent
 7. Scales of costae and costules pale at the bases and darker at the tips, conspicuously dentate **10. M. pulverulentum s.l.**
 7. Scales of costae and costules uniformly colored or slightly darker at the bases, subentire to moderately serrate
 8. Blades adaxially pubescent between and on the veins, the hairs ca. 1 mm long
 9. Rhizome scales golden-brown to pale brown under magnification and strong light, dark brown en masse
 10. Rhizome scales 1–2 mm wide **7. M. aureisquama**
 10. Rhizome scales to 1 mm wide **12. M. subincisum s.l.**
 9. Rhizome scales dark brown to blackish
 11. Abaxial blade surfaces densely pubescent; rhizome scales linear-lanceolate **8. M. ciliatum**
 11. Abaxial blade surfaces sparsely pubescent; rhizome scales lanceolate **11. M. marginatum**
 8. Blades adaxial glabrous or with a few hairs <0.5 mm long on veins and/or surfaces
 12. Short (0.2–0.5 mm long) hairs present abaxially on the veins and/or blade surfaces
 13. Blades densely covered with short hairs of about equal length; long hairs lacking **5. M. adenopteris**
 13. Blades with short hairs restricted to abaxial surfaces; long hairs on costules and veins present or lacking
 14. Costules, costae, and rachises abaxially glabrous or with scattered hairs 0.3–0.6 mm long **12. M. subincisum s.l.**
 14. Costules, costae, and usually rachises abaxially with dense hairs 0.05–0.2 mm long **13. M. vastum**
 12. Short hairs absent abaxially on veins and blade surfaces (may be present on the costae and costules)
 15. Rhizomes and basal petiole scales 1–2 mm wide, pale orange to golden brown under magnification and strong light, brown en masse, entire to finely serrate **7. M. aureisquama**
 15. Rhizomes and basal petiole scales to 1 mm wide, orange-brown under magnification and strong light, dark brown en masse, serrate
 16. Costal and costular scales linear-lanceolate, up to 10 cells wide **12. M. subincisum s.l.**
 16. Costal and costular cells broadly lanceolate, >10 cells wide
 17. Blades 3-pinnate-pinnatifid to four-pinnate; 2500–3000 m **6. M. alticola**
 17. Blades 2- to 3-pinnate; 1000–2000 m **11. M. rupicola**

PINNATE-PINNATIFID SPECIES

1. **Megalastrum biseriale** (Baker) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:127. 1987.

Polypodium biseriale Baker, Syn. fil. 309. 1867. TYPE.—Ecuador. Mt. Tungurahua, Spruce *s.n.* (holotype: K).

This species is recognized by a dense cover of very short hairs on the rachises, and orange to medium brown rhizome scales. It has short, appressed hairs on the costae, a thick laminar texture into which the ultimate veinlets are completely sunken (except for the hydathodes). In contrast to Tryon & Stolze (1991) who state that *M. biseriale* has a thin laminar texture, the Bolivian specimens placed under this name have the thickest laminar texture of any pinnate-pinnatifid species of *Megalastrum* in the country. We have also seen similar, thick-textured specimens from Colombia (*Herrera 9327*, UC) and Ecuador (*Neill 5956*, UC). Different taxa may be involved, but the taxonomy and nomenclature of this species group (including *M. honestum* and *M. yungense*) is complex and requires detailed work. In Bolivia, *M. biseriale* is known from five collections, all made at 1600–2900 m in and close to Cotapata National Park, Nor Yungas, La Paz.

SELECTED SPECIMENS EXAMINED.—Bolivia. **La Paz:** Prov. Nor Yungas, Estación Biológica de Tunquini, 16°11'S, 67°53'W, 1600 m, 22 Aug 2000, *Eberhardt 204* (LPB, UC); Prov. Nor Yungas, 19.8 km from Yolosa toward Chuspipata, 16°15'S, 67°45'W, 2280 m, 27 Jun 1989, *Fay & Fay 2205* (LPB, MO, UC).

2. **Megalastrum bolivianum** M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **Cochabamba:** Prov. Carrasco, 143 Km antigua carretera Cochabamba-Villa Tunari, 17°07'S, 65°34'W, 1300 m, 23 Aug 1996, *Kessler 7630a* (holotype: UC; isotypes: GOET, LPB). **Fig. 1 D–F.**

Megalastrum laminis pinnato-pinnatifidis, pilis strigosis albescentibus in costis venisque adaxialiter, squamis brunneis latis pilisque longis etiam brevibus in rhachidibus.

Terrestrial; rhizomes compact, scales linear-lanceolate, 5–8 × 0.5–0.8 mm, brown, clathrate, tortuous, remotely denticulate; petioles 10–13 cm × 1.5–2 mm, reddish brown, with dense scales similar to those of the petioles but smaller, and scattered hairs resembling those of the rachises; blades 22–27 × 8.5–10 cm, pinnate-pinnatifid, ovate-lanceolate, broadest at about 2/5 of the length; pinnae short-petiolate, to 5.2 × 1.8 cm, the proximal basispic and sometimes acroscopic segments enlarged except on the proximal pinnae; segments 3–4 mm wide, rounded to obtuse; rachises adaxially with dense, mixed indument consisting of reddish, spreading, septate, 5–8-celled hairs 0.8–1.3 mm, 1–2-celled reddish hairs 0.1–0.2 mm, and lanceolate, long-acuminate, brown, clathrate, remotely denticulate scales 1–3.5 × 0.2–0.7 mm, abaxially with similar scales but fewer, whitish hairs 0.5–1 mm; costae and veins adaxially with sparse, whitish, strigose hairs 1–1.5 mm, abaxially with moderately dense scales and hairs resembling those of the rachises abaxially,

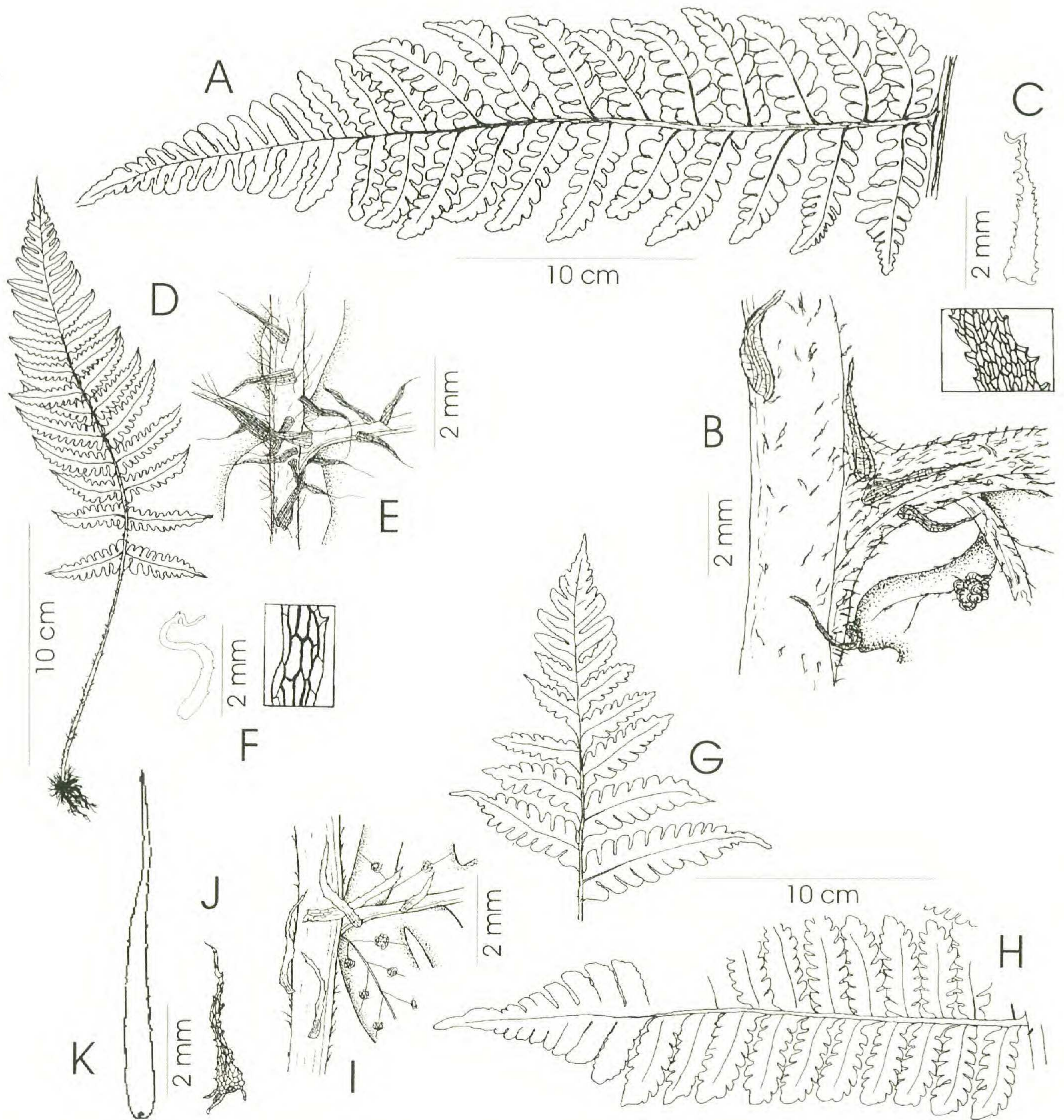


FIG. 1. A.–C. *Megalastrum alticola* M. Kessler & A.R. Sm. A. Proximal pinna. B. Rachis and pinna base. C. Costal scale with cell detail, *Kessler 11945* (UC). D.–F. *Megalastrum bolivianum* M. Kessler & A.R. Sm. D. Leaf. E. Rachis and pinna bases. F. Costal scale with cell detail, *Kessler 7630a* (UC). G.–J. *Megalastrum aureisquama* M. Kessler & A.R. Sm. G. Blade apex. H. Median pinna. I. Rachis and pinna base. J. Costal scale, K. Scale of petiole base, *Kessler 7379* (UC).

but shorter; laminar tissue thin, adaxially glabrous, abaxially with sparse, appressed, hyaline to orangish hairs 0.2–0.4 mm; veins dark, conspicuous; sori inframedial, 2–4 per segment, distributed along the entire segment, exindusiate.

PARATYPES.—Bolivia. **La Paz:** Prov. Nor Yungas, a 0.5 km de la Estación Biológica Tunquini, subiendo el Río Santa Catalina, 16°11'S, 67°52'W, 1600 m, 23 Aug 1998, *Portugal A. 246* (LPB, UC), *Portugal A. 269* (LPB).

This species is characterized by the long, whitish hairs on the veins of the adaxial blade surfaces, and by the mixture of long and very short hairs and broad, medium brown scales on the rachises. It is a small plant with thin blades and conspicuous, dark veins. The blade shape is ovate-lanceolate, rather than deltate as in most species of *Megalastrum*. Among the pinnate-pinnatifid species, the only other one with long hairs on the blades is *M. hirsutosetosum* (Hieron.) A.R. Sm. & R.C. Moran from Colombia to Ecuador; however, this species has longer, thinner, denser hairs on both sides of the blades. *Megalastrum bolivianum* is known from only three collections made at two sites in the departments of La Paz and Cochabamba in humid montane forests at 1300–1600 m.

3. *Megalastrum honestum* (Kunze) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:128. 1987.

Polypodium honestum Kunze, Linnaeae 9:49. 1834. TYPE:—Peru. **Dept. Huánuco:** Pampayacu, *Poeppig 22* (holotype: LZ, destroyed).

Of the pinnate-pinnatifid species, this is relatively large, and can be recognized by lacking hairs on the rachises (or with very few, scattered hairs), dark brown, long, narrow rhizome scales, and inframedial sori. It has thicker petioles than other Bolivian pinnate-pinnatifid congeners (basally to 6 mm thick vs. to 3–4 mm in the other species), and the basispic pinnule of each pinna is often enlarged (vs. not enlarged or enlarged only in the basalmost pinna pair in the other species). The application of the name *M. honestum* to Bolivian material is uncertain, because specimens cited below differ from Peruvian material in several conspicuous characters (larger size, different blade cutting with more pronounced basispic pinnules) not mentioned by Christensen (1913) or Tryon & Stolze (1991). Further, contrary to the statement in Tryon & Stolze (1991), the laminar texture of *M. honestum* is thinner than that of *M. biseriale*. We have been unable to locate type material of *M. honestum* (the holotype was destroyed at LZ, and no isotypes are known to us), and the matter may therefore be impossible to settle. Pending a thorough revision of the genus, we tentatively apply the name to specimens cited below. In Bolivia, *M. honestum* is known from eleven collections made in humid foothill forests at 450–1700 m in the departments of Beni, La Paz, Cochabamba, and Santa Cruz.

SELECTED SPECIMENS EXAMINED.—Bolivia. **Beni:** Prov. Ballivián, 16 km por camino maderero al SW del Km 12 Yucumo-Rurrenabaque, 15°5'S, 67°7'W, 800 m, 03 Aug 1997, *Kessler 10982* (GOET, LPB, UC). **Cochabamba:** Prov. Carrasco, Parque Nacional Carrasco, al S del Campamento Petrolero Ichoa, 17°23'S, 64°30'W, 440 m, 15 Sep 1997, *Acebey 595* (LPB, UC). **La Paz:** Prov. Caranavi, Serranía Bellavista, 46 km Caranavi a Sapecho, 15°39'S, 67°28'W, 1200 m, 30 Aug 1997, *Kessler 11604* (GOET, LPB, UC). **Santa Cruz:** Prov. Ichilo, 4 km SW del Campamento Macuñucú, 17°44'S, 63°35'W, 450 m, 27 Sep 1996, *Kessler 8680* (GOET, LPB, UC).

4. **Megalastrum yungense** (H. Christ & Rosenst.) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:129. 1987.

Dryopteris yungensis H. Christ & Rosenst., Repert. Spec. Nov. Regni Veg. 5:234. 1908. TYPE:—Bolivia. **La Paz**: Prov. Sud Yungas, Sirupaya, Yanacachi, 2000 m, *Buchtien 493* (holotype: P; isotype: US).

This rare endemic species, known from only two collections, differs from *M. honestum* by its broader, paler rachis scales and supramedial (vs. inframedial) sori (Christensen 1920). It is also a smaller species with less pronounced basispic pinnules. A specimen from Peru (*Smith 4424*, UC) was placed under this species by Tryon & Stolze (1991), but it has densely hairy rachises and thus falls within our concept of *M. biseriale*.

SPECIMEN EXAMINED.—Bolivia. **Beni**: Prov. Ballivián, 138 km N of Caranavi, 15°12'S, 67°3'W, 700 m, 20 Jun 1989, *Fay & Fay 2051* (LPB, MO).

DECOMPOUND SPECIES

5. **Megalastrum adenopteris** (C. Chr.) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:127. 1987.

Dryopteris adenopteris C. Chr., Kongel. Dankse Vidensk. Selsk. Skr., Naturvidensk Math. Afd., ser. 8. 6:85. 1920. Type:—Brazil (South). *Lindman A1313* (holotype: S).

This species, otherwise known from southern Brazil and northern Argentina, is characterized by its short hairs on both blade surfaces; it does not present taxonomic problems in Bolivia. Bolivian specimens have very small indusia that may be hard to see in sori with fully developed sporangia. *Megalastrum adenopteris* is known in Bolivia from three collections (two of which are cited in Smith *et al.* 1999) in semihumid forests at 890–1750 m in Santa Cruz and Tarija departments.

SPECIMEN EXAMINED.—Bolivia. **Tarija**: Prov. A. Arce, P.N. Tariquía, campamento de guardaparques Sidras, senda La Cascada, 22°14'S, 64°32'W, 890 m, 19 Jun 2004, *Jimenez 2468* (GOET, LPB, UC).

6. **Megalastrum alticola** M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **La Paz**: Prov. Nor Yungas, 2 km de Chuspipata hacia Coroico, 16°22'S, 67°49'W, 2900 m, 17 Sep 1997, *Kessler 11945* (holotype: UC; isotypes: GOET, LPB). **Fig. 1 A–C.**

A *Megalastrum subinciso* (Willd.) A.R. Sm. & R.C. Moran squamis costarum costularumque latioribus (plus 10 cellulas vs. minus 10 cellulas latis), a *M. rupicola* M. Kessler & A.R. Sm. foliis majoribus subtilioribus dissectis, squamis rhizomatum petiolorumque majoribus differt.

Terrestrial; rhizomes compact, scales linear-lanceolate, 13–25 × 0.5–1 mm, shiny orange-brown, clathrate, erose-denticulate; petioles to 95 cm × 15 mm, basally reddish brown, distally stramineous, shiny when scurf abraded, scales

dense at bases, otherwise petioles covered by a dense scurf of appressed, reduced scales; blades to ca. 120×90 cm, 3-pinnate-pinnatifid, deltate, the lowermost pinnae the longest; pinnae to ca. 45×20 cm, the proximal basispic pinnules enlarged especially on the proximal pinnae; ultimate segments 1.5–3 mm wide, rounded to obtuse; rachises adaxially densely short-hairy along the grooves, otherwise sparsely scaly, the scales $0.2\text{--}3 \times 0.1\text{--}1$ mm, brown, subclathrate, erose-denticulate; costae, costules, and veins adaxially with dense, reddish hairs 0.2–0.4 mm, on veins hairs to 0.7 mm long, abaxially with moderately dense, brown, clathrate, ovate-lanceolate, erose-denticulate scales >10 cells wide, $0.3\text{--}1.2 \times 0.6\text{--}1.5$ mm, and moderately dense, pale reddish hairs to 0.2–0.5 mm; laminar tissue adaxially glabrous, abaxially with scattered, appressed, reddish hairs 0.2–0.4 mm, margins with regularly spaced, whitish hairs 0.3–0.6 mm; sori inframedial, 1–3 per segment, mostly restricted to segment bases, exindusiate.

PARATYPES.—Bolivia. **Cochabamba:** Prov. Carrasco, Km 108 antigua carretera Cochabamba a Villa Tunari, $17^{\circ}9'S$, $65^{\circ}38'W$, 2950 m, 22 Jun 1996, *Kessler 6539* (GOET, LPB, UC); same general locality, Km 115, $17^{\circ}8'S$, $65^{\circ}38'W$, 2500 m, 04 Jul 1996, *Kessler 6964* (GOET, LPB, UC); same locality, 2600 m, 05 Jul 1996, *Kessler 7014* (GOET, LPB, UC).

This species differs from *M. subincisum* by its broader costal and costular scales (scales >10 cells wide vs. <10 cells wide) and from *M. rupicola* by its larger size with more finely dissected blades, and larger rhizome and petiole scales. It occurs at higher elevations (2500–2950 m) than any other Bolivian *Megalastrum* except *M. aureisquama*. In contrast, *M. subincisum* is found from 250–2250 m. Two of the four known collections have apparently mature, but malformed sporangia, but in the type collection the sporangia and spores appear well-developed. Whether the malformed sporangia are a result of hybridization (but with which parent taxa is unclear, considering that at such high elevations there is only one other, quite different species of the genus) or of environmental stress at the upper elevational limit of the genus is unknown.

7. *Megalastrum aureisquama* M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **Cochabamba:** Prov. Carrasco, 137 Km antigua carretera Cochabamba-Villa Tunari, $17^{\circ}06'S$, $65^{\circ}35'W$, 1600 m, *Kessler 7379* (holotype: UC; isotypes: GOET, LPB). **Fig. 1 H–K.**

A *Megalastrum subinciso* (Willd.) A.R.Sm. & R.C. Moran squamis rhizomatum petiolorum inferiorisque latissimis (1–2 mm), nitentibus, obscure aureobrunneis, integris usque subtiliter serratis differt.

Terrestrial; rhizomes compact, scales linear-lanceolate, $10\text{--}20 \times 1\text{--}2$ mm, shiny, dark golden-brown, subclathrate, entire to finely serrate; petioles to $90\text{+ cm} \times 18$ mm, brown, densely covered with an appressed scurf of dissected scales, bases with dense scales resembling those of the rhizomes but smaller; blades known from incomplete material, at least to 120×50 cm, probably deltate, basally 3-pinnate; pinnae short-petiolate, at least to 28×15 cm; segments 3–6 mm wide, rounded to obtuse; rachises adaxially with dense, pale

reddish hairs 0.5–1 mm along the grooves, otherwise covered with an appressed scurf of dissected scales and moderately dense, linear-lanceolate, shiny, dark golden-brown, subclathrate, entire to finely serrate scales 5–10 × 0.4–1 mm; costae and veins adaxially with moderately dense, pale reddish hairs 0.4–0.7 mm, abaxially with moderately dense, appressed, linear-lanceolate, shiny, dark golden-brown, subclathrate, entire to finely serrate scales 2–6 × 0.2–0.7 mm; laminar tissue glabrous on both sides or adaxially with sparse, strigose, whitish hairs 0.5–1 mm; sori supramedial, 4–8 per segment, distributed along the entire segment, exindusiate.

PARATYPES.—Bolivia. **Cochabamba:** Prov. Carrasco, Km 113 antigua carretera Cochabamba a Villa Tunari, 17°7'S, 65°38'W, 2600 m, 03 Jul 1996, *Kessler 6908* (GOET, LPB, UC); same general locality, Km 116, 17°8'S, 65°38'W, 2400 m, 06 Jul 1996, *Kessler 7033* (GOET, LPB, UC); same general locality, Km 130, 17°7'S, 65°36'W, 2000 m, 11 Jul 1996, *Kessler 7185* (GOET, LPB, UC); same general locality, Km 100, 17°11'S, 65°38'W, 3200 m, 20 Aug 1996, *Kessler 7522* (GOET, LPB, UC); same general locality, Km 143, 17°7'S, 65°34'W, 1300 m, 23 Aug 1996, *Kessler 7644* (GOET, LPB, UC); same general locality, Km 134, 17°7'S, 65°34'W, 1650 m, 26 Aug 1996, *Kessler 7789* (GOET, LPB, UC).

This species is readily recognized by its very broad, shiny, dark golden-brown, entire to finely serrate rhizome and basal petiole scales. Similar, but smaller scales are found on the rachises, costae, and costules. It is probably most closely related to *M. subincisum*, but that species has much narrower, darker, and more strongly denticulate rhizome and petiole scales. In *M. aureisquama*, most specimens found below 2000 m are glabrous on the adaxial blade surfaces, whereas most high-elevation specimens have long hairs on the costules and veins. *Megalastrum aureisquama* is fairly common at 1300–3200 m in humid montane forests in the very wet Chapare region of Dpto. Cochabamba.

8. *Megalastrum ciliatum* M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **La Paz:** Prov. Sud Yungas, camino Chulumani-Ocobaya, 2.5 km después de Chulumani, 1600 m, *Schmit 422* (holotype UC; isotype LPB). **Fig. 2 A–C.**

Megalastrum foliis tripinnato-pinnatifidis, pilis longis adaxialiter in venis, abaxialiter etiam inter venas instructis, squamis costalibus denticulatis, iisdem rhizomatum subtiliter ciliatis notatum.

Terrestrial; rhizomes compact, scales linear-lanceolate, 8–14 × 1–2 mm, shiny, dark brown, not clathrate, short-ciliate; petioles 33 cm × 4 mm, stramineous, shiny, scales basally dense, distally scattered, appressed and reduced in size; blades known only from incomplete material, 45+ × ca. 40 cm, probably deltate, basally 3-pinnate, the lowermost or the 2nd pinna pair the longest; pinnae short-petiolate, to 23 × 12 cm, the proximal basisopic segments enlarged especially on the proximal pinnae; segments 3–5 mm wide, rounded to obtuse; rachises adaxially densely hairy along the grooves, the hairs pale orangish, 0.6–1.2 mm long, otherwise sparsely hairy and scaly, the scales 1–3 × 0.1–0.4 mm, dark brown, not clathrate, denticulate; costae and veins

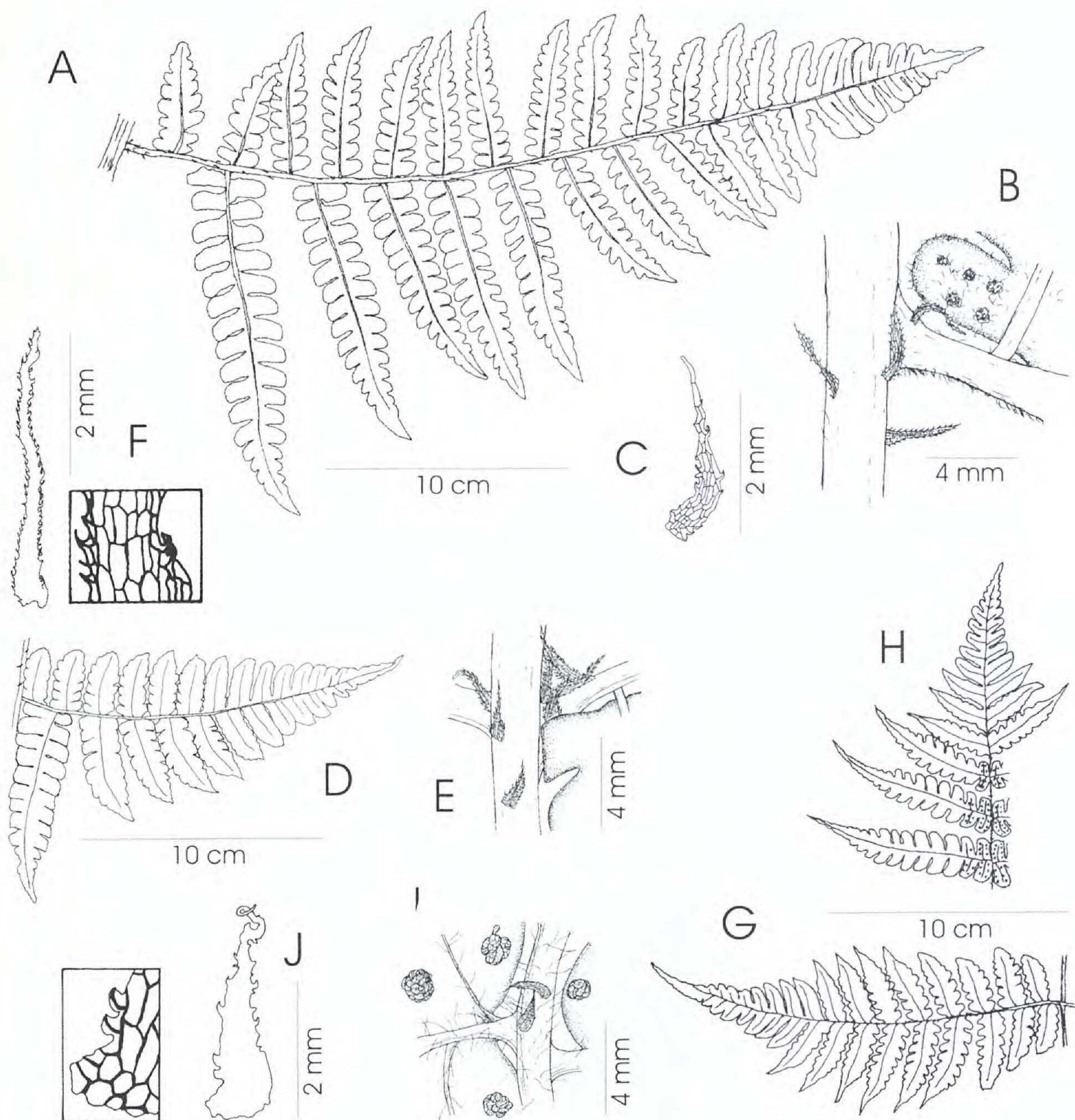


FIG. 2. A.-C. *Megalastrum ciliatum* M. Kessler & A.R. Sm. A. Proximal pinna. B. Rachis and pinna base. C. Costal scale, *Schmit 422* (UC). D.-F. *Megalastrum rupicola* M. Kessler & A.R. Sm. D. Proximal pinna. E. Rachis and pinna bases. F. Costal scale with cell detail, *Quintana 41* (UC). G.-J. *Megalastrum marginatum* M. Kessler & A.R. Sm. G. Blade apex. H. Median pinna. I. Rachis and pinna base. J. Costal scale with cell detail, *Portugal 538* (UC).

adaxially strigose with moderately dense, whitish hairs 0.5–0.8 mm, abaxially with moderately dense, lax, spreading, whitish hairs 0.5–0.8 mm, and with scattered scales resembling those of the rachises but smaller; laminar tissue adaxially glabrous, abaxially moderately hairy with hairs similar to those of the veins; sori medial, 4–6 per segment, distributed along the entire segment, exindusiate.

This species is characterized by 3-pinnate leaves with long hairs on the blades adaxially and abaxially (both on and between the veins), denticulate, concolorous costal scales, and dark brown, finely ciliate rhizome scales. It may

be closest to *M. pulverulentum*, but that species has strongly bicolorous costal scales with much coarser teeth. *Megalastrum ciliatum*, named for its short-ciliate rhizome scales, is known only from the type collection in secondary humid montane forests near the town of Chulumani on a semi-isolated mountain range in the Bolivian Yungas. This range supports a number of locally endemic plant taxa (S.G. Beck, pers. comm.), and the present species may also be restricted to this area.

9. *Megalastrum marginatum* M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **La Paz:** Prov. Nor Yungas, Cerro Hornuni, 16°01'S, 67°52'W, 1850 m, 27 Nov 1998, *Portugal 538* (holotype: UC; isotype: LPB). **Fig. 2 D–F.**

A *Megalastrum rupicola* M. Kessler & A.R.Sm. in foliis basaliter tripinnatis, pilis longis costis venisque ambarum paginarum laminarum, squamis rhizomatum brevioribus fuscioribusque, soris supramedialis positis differt.

Terrestrial; rhizomes compact, scales linear-lanceolate, 5–10 × 0.2–0.6 mm, shiny brown, subclathrate, remotely denticulate; petioles 30 cm × 3 mm, basally brown, distally stramineous, shiny, scales basally dense, distally scattered and reduced in size; blades 50 × 35 cm, deltate, basally 3-pinnate, the lowermost pinnae the longest; pinnae sessile, to 17 × 13 cm, the proximal basiscopic segments enlarged, especially on the proximal pinnae; segments 3–5 mm wide, obtuse; rachises adaxially densely hairy along the grooves, otherwise sparsely scaly, the scales 1–3 × 0.1–0.8 mm, brown, clathrate, denticulate, sometimes with a few admixed hairs; costae and veins adaxially with moderately dense, whitish hairs 1–1.5 mm, abaxially with similar but somewhat sparser and shorter hairs and with scattered scales resembling those of the rachises but smaller; laminar tissue glabrous on both sides; sori supramedial, 2–8 per segment, distributed along the entire segment, exindusiate.

PARATYPE.—Bolivia. **La Paz:** Prov. Sud Yungas, camino Chulumani-Ocobaya, 2.5 km después de Chulumani, 16°25'S, 67°31'W, 1600 m, 01 Jun 1992, *Schmit 440* (LPB).

This species is most similar to *M. rupicola*, with which it grows, but differs by its basally 3-pinnate blades, long hairs on the costae and veins on both sides of the blades, shorter and darker rhizome scales, and supramedial sori. *Megalastrum marginatum* is known from only two collections made in humid montane forests (the type was found along a creek) at 1600–1850 m.

10. *Megalastrum pulverulentum* (Poir. in Lam.) A.R. Sm. & R.C. Moran, s.l., Amer. Fern J. 77:129. 1987.

Polypodium pulverulentum Poir. in Lam., Encycl. Méth. 5:555. 1804. TYPE.—*Plumier*, Traité foug. Amér. t. 34, 1705, based on a plant from Hispaniola.

On average, Bolivian specimens of this widespread species have shorter rachis and petiole scales than specimens from northern South America and Mesoamerica (although the extremes overlap). Only one specimen (*Kessler*

9088, LPB, GOET, UC) has scales approaching those of typical, northern *M. pulverulentum*. Within Bolivia, two morphologically and geographically distinct populations can be distinguished. One (morph 1) occurs in south-central Bolivia and bears long hairs on the adaxial leaf surfaces. The other (morph 2) is found in central Bolivia and has almost glabrous adaxial and abaxial leaf surfaces, as well as slightly broader scales on the rhizomes and petiole bases. These forms may warrant treatment as distinct taxa, but detailed studies throughout the range of the species (or species complex) is needed to adequately evaluate its morphological variability. For example, some specimens of morph 2 closely resemble *M. pulverulentum* var. *heydei* (C. Chr.) A.R. Sm. & R.C. Moran of Mesoamerica, but the similarity is probably superficial. In Bolivia, *M. pulverulentum* is known from 23 collections made in humid forests at (400)1000–2900 m in the departments of Chuquisaca, Cochabamba, and Santa Cruz.

SELECTED SPECIMENS EXAMINED.—Bolivia. **Chuquisaca:** Prov. Calvo, Ñahuañanca, 19°18'S, 63°44'W, 1061 m, 08 Jul 2001, *Huaylla 211* (LPB) (morph 1). **Cochabamba:** Prov. Carrasco, Km 130 antigua carretera Cochabamba a Villa Tunari 17°7'S, 65°36'W, 2000 m, 11 Jul 1996, *Kessler 7188* (GOET, LPB, UC) (morph 2); Prov. Carrasco, 10 km aproximadamente desde el campamento Israel en dirección al Río Sacta, entrando a la confluencia del límite del Parque Nal. Carrasco y el Río Zabala, 17°17'S, 64°52'W, 400 m, 19 Jan 2000, *Jimenez 224* (AAU, LPB) (morph 2). **Santa Cruz:** Prov. Valle Grande, Loma Larga, 1 km a Masicurí, 18°46'S, 63°54'W, 1900 m, 29 May 1996, *Kessler 6171* (LPB, UC) (morph 1); Prov. Florida, Parque Nacional Amboró, 7 km NNE by air from Mairana, 18°3'S, 65°55'W, 2000 m, 23 Jul 1994, *Moran 5911* (UC) (morph 1).

11. *Megalastrum rupicola* M. Kessler & A.R. Sm., *sp. nov.* TYPE.—Bolivia. **La Paz:** Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 16°12'S, 67°53'W, *Quintana 41* (holotype: UC; isotypes: GOET, LPB). **Fig. 6.**

A Megalastro subinciso (Willd.) A.R. Sm. & R.C. Moran squamis costarum costularumque valde latioribus, pallidioribus, translucetioribus differt; etiam ad staturam minorem segmentos ultimosque obtusiores quam *M. subincisum* tendens.

Terrestrial; rhizomes compact, scales linear-lanceolate, 8–17 × 0.3–0.8 mm, shiny orange-brown, clathrate, remotely denticulate; petioles 30–60 cm × 3–8 mm, basally rich brown, distally stramineous, shiny, scales basally dense, distally scattered and reduced in size; blades 40–80 × 30–50 cm, 2-pinnate-pinnatifid, deltate, the lowermost pinnae the longest; pinnae short-petiolate, to 15 × 8.5 cm, the proximal basisopic segments enlarged especially on the proximal pinnae; segments 2.5–5 mm wide, rounded to obtuse; rachises adaxially densely short-hairy along the grooves, otherwise sparsely scaly, the scales 0.2–4.5 × 0.1–0.8 mm, brown, clathrate, denticulate, sometimes with a few admixed hairs; costae and veins adaxially with dense, reddish hairs 1–1.5 mm, abaxially with scattered brown, clathrate, denticulate scales

0.2–3 × 0.1–0.8 mm, and scattered whitish, spreading hairs to 1 mm; laminar tissue glabrous on both sides or with very few hairs to 1 mm; sori medial, 2–10 per segment, distributed along the entire segment, exindusiate.

PARATYPES.—Bolivia. **Cochabamba:** Prov. Chapare, Territorio Indígena Parque Nacional Isiboro-Sécure, Cordillera de Mosetenes, arriba de la Laguna Carachupa, 16°14'S, 66°25'W, 1350 m, 30 Aug 2003, *Kessler 13070* (LPB, UC). **La Paz:** Prov. B. Saavedra, Pauji-Yuyo, entre Apolo y Charazani, 15°2'S, 68°29'W, 1050 m, 08 Jun 1997, *Kessler 9900* (GOET, LPB, UC); Prov. Nor Yungas, Estación Biológica de Tunquini, Hornuni Bajo, senda del campo de Don Pedro al pajonal atrás del Río Cedroni, 16°42'S, 67°52'W, 1900 m, 24 Jul 2001, *Bach 1234* (GOET, LPB, UC); Estación Biológica de Tunquini, 16°11'S, 67°53'W, 1600 m, 18 Aug 2000, *Eberhardt 142* (LPB, NY, UC); same locality, 1690 m, 22 Aug 1999, *Portugal 223* (LPB, UC), 1680 m, 10 Mar 1998, *Portugal 366* (LPB, UC), 1680 m, 10 Mar 1998, *Portugal 368* (LPB), 1680 m, 10 Mar 1998, *Portugal 370* (LPB, UC), 1760 m, 10 Apr 1998, *Portugal 401* (LPB, UC), 1790 m, 10 Jul 1998, *Portugal 452* (LPB, UC).

This species differs from *M. subincisum* by its broader, paler, more translucent costal and costular scales. It also tends to be smaller and to have blunter ultimate segments than *M. subincisum*. The proximal pinnae of *M. rupicola* typically are slightly falcate. We include here specimens reported as *M. connexum* (Kaulf.) A.R. Sm. & R.C. Moran *vel aff.* by Smith *et al.* (1999). However, material of *M. connexum* from southeastern Brazil and Paraguay has much fewer, paler, less spreading, and laxer scales. One collection (*Eberhardt 402*, UC) is morphologically intermediate between *M. rupicola* and *M. subincisum* and has malformed sporangia; it may represent a hybrid. *Megalastrum rupicola* is a locally common species at 1050–1900 m in humid montane forests, especially along streams.

12. *Megalastrum subincisum* (Willd.) A.R. Sm. & R.C. Moran, s.l., Amer. Fern J. 77:129. 1987.

Polypodium subincisum Willd., L. Sp. Pl. ed. 4, 5:202. 1810. TYPE.—Venezuela. Caracas, *Bredemeyer s.n.* (holotype: B, *Herb. Willd. 19701*; photos F, US).

Throughout its extensive range (Mexico and West Indies to Bolivia) this species varies considerably in size, blade dissection, and length and density of hairs on the blades; Further studies may reveal it to be a species complex. Usually, the leaves are glabrous except for dense, short hairs on the costae and costules on both leaf surfaces and for scattered short hairs on the segment margins. However, several Bolivian specimens clearly stand apart: one morph (*Kessler 10897, 11131*) has scattered, very short, erect hairs on the abaxial leaf surfaces between the veins, whereas yet another form (*Acebey 730, Krömer 100*) has long hairs on the costules and veins of the adaxial leaf surfaces. In Bolivia, it is known from 24 collections in humid forests at 250–2250 m in the departments of Beni, Cochabamba, La Paz, and Santa Cruz.

SELECTED SPECIMENS EXAMINED.—Bolivia. **Beni:** Prov. Ballivián, Km 16 por camino maderero al SW del Km 12 Yucumo-Rurrenabaque, 15°5'S, 67°7'W, 700 m, 31 Jul 1997, *Kessler 10897* (GOET, LPB, UC); Puente Río Quiquibey 4 kms hacia San Borja, 700 m, 14 Jul 1979, *Beck 1705* (LPB, UC). **Cochabamba:** Prov. Carrasco, Parque Nacional Carrasco, al S del Campamento Petrolero Ichoa, 17°23'S, 64°23'W, 660 m, 21 Sep 1997, *Acebey 730* (LPB, UC); Prov. Ayopaya, Comunidad Pampa Grande, subiendo por el lecho del primer afluente que uno encuentra al cruzar y subir por el Río Pampa Grande, 16°40'S, 66°28'W, 2260 m, 15 Sep 2002, *Jimenez 1641* (LPB, UC). **La Paz:** Prov. Iturrealde, Río San Antonio, 46 km de Ixiamas a Alto Madidi, 13°38'S, 68°26'W, 300 m, 13 Aug 1997, *Kessler 11131* (GOET, LPB, UC); Prov. Sud Yungas, Alto Beni, Sapecho, Colonia Tupiza, 15°32'S, 67°18'W, 735 m, 29 Oct 1997, *Krömer 100* (GOET, LPB, UC); Prov. Caranavi, Serranía Bellavista, 46 km Caranavi a Sapecho, 15°39'S, 67°28'W, 1200 m, 30 Aug 1997, *Kessler 11621* (GOET, LPB, UC). **Santa Cruz:** Prov. Ñuflo de Chávez, Serranía San Lorenzo, 2 km E of Estancia Las Maras, 16°15'S, 62°35'W, 700 m, 03 Nov 1985, *Killeen 1383* (LPB, UC).

13. *Megalastrum vastum* (Kunze) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:129. 1987.

Polypodium vastum Kunze, Linnaea 9:50. 1834. TYPE.—Peru. **Dpto. Huánuco:** inter Pampayacu et Cocheros et ad Ventanilla de Cassapi, *Poeppig 217* (holotype: B; isotypes: B, L; photos F, US of L).

This species is closely related to *M. subincisum*, but differs by its dense, regularly spaced, 0.05–0.2 mm long hairs on the costae, costules, and usually rachises abaxially. Given the variability of *M. subincisum*, some specimens of that species approach *M. vastum*, and the distinction between these species is not always clear. *Megalastrum vastum* is a rare species in Bolivia, being known from only three collections made in humid forests at 1100–1300 m in the departments of Cochabamba and La Paz. We have not examined two collections cited by Christensen (1920): La Paz: Prov. Nor Yungas, Polo-Polo prope Coroico, 1100 m, 1912, *Buchtien 3588* (R), *3609* (R).

SELECTED SPECIMEN EXAMINED.—Bolivia. **Cochabamba:** Prov. Chapare, Territorio Indígena Parque Nacional Isiboro-Sécure, Cordillera de Mosetenes, Laguna Carachupa, 16°14'S, 66°25'W, 1300 m, 29 Aug 2003, *Kessler 12995* (LPB, UC).

14. *Megalastrum villosulum* (C. Chr.) A.R. Sm. & R.C. Moran, Amer. Fern J. 77:129. 1987.

Dryopteris villosula C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Math. Afd., ser. 8. 6:89. 1920. TYPE.—Bolivia. **La Paz:** Prov. Nor Yungas, Uchumachi, *Bang 2394* (holotype: B; isotypes: NY, US).

This endemic and distinctive species is the only persistently and conspicuously indusiate *Megalastrum* in Bolivia. It is probably closely related to *M. andicola* (C. Chr.) A.R. Sm. & R.C. Moran from Colombia, Ecuador, and Peru, which may be expected also to occur in Bolivia. It differs from *M. villosulum* by lacking small, appressed, glandular hairs on the abaxial blade surfaces and instead bearing dense, long hairs. Until a few years ago, *M. villosulum* was known only from the type collection, but we now have seen five gatherings from humid montane forests at 1800–2150 m in the departments of La Paz, Cochabamba, and Santa Cruz.

SELECTED SPECIMENS EXAMINED.—Bolivia. **Cochabamba:** Prov. Ayopaya, Comunidad Pampa Grande, subiendo por el sendero río arriba, pasando la primera área de cultivo, 16°40'S, 66°28'W, 2150 m, 09 Jul 2002, *Jimenez 1428* (LPB, UC). **La Paz:** Prov. F. Tamayo, Parque Nacional Madidi, Quebrada Jatun Chiriuno, 31 km en línea recta al E de Apolo por el camino a San José, 14°30'S, 68°14'W, 1850 m, 19 Jul 2002, *Fuentes 5131* (LPB, UC). **Santa Cruz:** Prov. Valle Grande, Loma Larga, 5 km a Vallegrande, 18°43'S, 63°54'W, 2100 m, 08 Jun 1996, *Kessler 6379* (LPB, UC).

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